

Ingestion of leaf litter by millipedes: The accuracy of laboratory estimates for predicting litter turnover in the field

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The activities of soil macrofauna can influence the rates of organic matter decomposition (Peterson & Luxton 1982). For example, in many natural habitats epigeic and anecic species may consume up to 30% of the litter standing crop (Swift, Heal & Anderson 1979). The consumption of leaf litter also affects the activities of bacteria and fungi and can alter the spatial distribution of nutrients (Anderson 1988a, b).

In order to establish the relative importance of litter feeding animals for nutrient dynamics within ecosystems estimates of total ingestion of leaf litter are necessary. There are considerable difficulties in obtaining such data under field conditions and most studies, with the notable exception of those on termites (for example, Collins 1981), have resorted to laboratory estimates of ingestion rates (see references in Table 2). This note considers the accuracy of such estimates when they are used to predict leaf litter consumption under field conditions and questions the importance of coprophagy as a digestive tactic in millipedes. Feeding experiments were conducted (Dangerfield & Milner 1993) in which ground leaf litter from the canopy tree *Combretum erythrophyllum* (Burch.) was presented to individuals of four spirostreptid millipedes: *Alloporus uncinatus* (Attems), *Paratophius* sp., *Odontopyge* sp. 2 and *Odontopyge* sp. 3 (species definitions follow Dangerfield & Telford 1992) in a palatability design. Each animal was weighed and placed in 16 cm diameter plastic bowls containing between 2.0 and 10.0 g dry mass of hand crushed and sieved (2.00 mm) leaf litter. In order to minimise mortality, approximately 5 cm³ of water was added to all replicates every 3 days using a fine nozzle wash bottle and to maintain even humidity all bowls were loosely covered with a sheet of clear plastic. Ingestion was estimated gravimetrically after 7 weeks taking into account mass loss from litter due to microbial activity (further experimental details in Dangerfield & Milner 1993). During the first two weeks of the experiment faecal pellets were removed daily to estimate pellet production rate, thereafter the animals had access to their faeces. The pellets were dried and weighed individually hence ingestion could also be estimated from the expected mass of faecal pellets produced per day.

Ingestion rates based on gravimetric analyses (I_g), that is, the dry mass of litter presented minus the litter not consumed, and estimates of ingestion based on faecal pellet production (I_p) are given in Table 1. Even given the assumption that none of the litter ingested was assimilated ingestion based on pellet production was 3 to 6 times higher than gravimetric estimates where animals had access to their faeces. McBrayer (1973) showed similar results with a two-fold increase in ingestion from 30 mg day⁻¹ of leaf litter to 67 mg day⁻¹ when individuals of the temperate species *Apheloria montana* (Bollman) were denied access to their faeces. If prolonged confinement reduced ingestion rates the I_p would be overestimated. Such a decline occurred in *Paratophius* sp. (pellet production = 5.81 ± 0.111 time, $r = 0.362$, $P < 0.02$, $n = 42$), however, integrating this decline resulted in mean daily pellet production of 2.93 day⁻¹ over seven weeks, still 4.0 times higher than the gravimetric estimate (Table 1). Mean daily pellet production did not decline significantly over the 14 days of measurements in *Odontopyge* sp. 2 ($r = 0.227$, $P > 0.1$, $n = 22$) or *A. uncinatus*

($r = 0.212$, $P > 0.1$, $n = 22$) and in *Odontopyge* sp. 3 there was a significant increase over time ($r = 0.475$, $P < 0.05$, $n = 22$). These results strongly suggest that the animals consume their faeces.

In several studies of temperate millipede species the experimental design allowed animals access to faeces and in some cases mineral soil. The ingestion rates quoted in these experiments (Table 2) are broadly similar to the gravimetric estimates given here. Of the published information only in a study by Neuhauser & Hartenstein (1978) did the experimental design prevent coprophagy, however, mass specific estimates of ingestion were

Table 1. Differences in the estimates of ingestion from gravimetric analyses (I_g) where animals had access to their faeces and estimates based on faecal pellet production (I_p) for four species of spirotreptid millipede

	body mass (g dry mass)	I_g (mg/day)	mean pellets per day	pellet mass	pellet production* (mg/day)	I_p/I_g
<i>Odontopyge</i> sp. 3	0.44 ± 0.04	30	7.5	11.5	86	2.9
<i>Odontopyge</i> sp. 2	0.88 ± 0.10	34	11.1	20.3	225	6.6
<i>Paratopophilus</i> sp.	0.98 ± 0.06	32	4.2	44.2	186	5.8
<i>Alloporus uncinatus</i>	2.86 ± 0.14	75	5.6	62.9	352	4.7

* Pellet production is used here as an estimate of ingestion (I_g) given the conservative assumption that none of the leaf litter is assimilated

Table 2. Laboratory estimates of maximum leaf litter consumption (C) by various millipede species

Species	C (mg/day)	access to faecal pellets	Source
<i>Rossius</i> <i>kessleri</i>	78	(yes)	Striganova & Prishatova (1990)
<i>Orthoporus</i> <i>ornatus</i>	65	yes	Wooten & Crawford (1975)
<i>Sarmatius</i> <i>kessleri</i>	63	(yes)	Striganova (1972)
<i>Schizophyllum</i> <i>caspium</i>	25	(yes)	Striganova & Rachmanov (1972)
<i>Orthomorpha</i> <i>gracilis</i>	12	yes	Kheirallah (1978)
<i>Glomeris</i> <i>balkanica</i>	11	(yes)	Iatrou & Stamou (1988)
<i>Amblyulus</i> <i>continentalis</i>	10	(yes)	Striganova & Rachmanov (1972)
<i>Chromatoiulus</i> <i>projectus</i>	8	yes	Pobozsny (1986)
<i>Cylindroiulus</i> <i>luridus</i>	7	yes	Pobozsny (1986)
<i>Leptoiulus</i> <i>proximus</i>	6	yes	Pobozsny (1986)
<i>Chromatoiulus</i> <i>projectus</i>	5	yes	Pobozsny (1985)
<i>Glomeris</i> <i>hexasticha</i>	4	yes	Gere (1956)
<i>Chromatoiulus</i> <i>projectus</i>	2	yes	Gere (1956)

presented (maximum 4.31 mg/g/day) and the size of the experimental animals was not recorded. Most other studies do not state whether coprophagy was possible but produced results of less than 40 mg/day ingested (Table 2). Coprophagy or consumption of soil (Dangerfield 1993) in the confined conditions of laboratory cultures drastically reduces ingestion of leaf litter.

Although a wide range of material is ingested by millipedes, including mineral soil, there have been no field records of animals consuming their own faeces. Recently over 450 field observations of millipede feeding behaviours in *Acacia* savanna produced no evidence of feeding on millipede faeces (Dangerfield, Milner & Matthews 1993; Dangerfield unpublished data). It is unlikely that such a food source would have been overlooked or mistaken as faecal pellets from southern African spirostreptids are of considerable size (50–150 mm³) and, due to a high carbon content, are much darker in colour than the surrounding soil or leaf litter.

In a riparian habitat at Mazowe, Zimbabwe, *A. uncinatus* formed aggregates of up to 40, mainly immature, individuals which were persistent on given microsites for several weeks (Dangerfield & Telford 1993). A large volume of faecal pellets accumulated at each of these microsites but none were consumed by the animals during the periods of observation. Although coprophagy is certainly a significant and potentially adaptive behaviour for detritivores (Hassall & Rushton 1982) its importance may be overestimated in the confined conditions of laboratory cultures. The restricted choice of food in palatability designs may make coprophagy more attractive than the available alternatives. The wider range of potential food sources available in the field may lessen the value of reingesting food to the extent that it becomes relatively unimportant component of the diet. This may be particularly so during periods of surface activity when active foraging and consumption of nutritious foods, such as fallen fruits, is common (Dangerfield & Telford 1991). When animals are confined by environmental conditions to specific shelter sites faecal pellets may again become a valuable food source.

The implications of these observations are that ingestion of leaf litter and subsequent faecal pellet production by detritivores may be much higher under natural conditions than predictions extrapolated from data on ingestion obtained in laboratory studies. This suggestion is consistent with recent estimates by Schaefer (1990) that litter consumption by detritivores in a temperate beech forest was of the same order of magnitude as the annual litter fall. In future studies it may be instructive to include within the standard palatability or feeding preference experimental designs measurements of ingestion and daily pellet production from animals denied access to faeces.

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